SUMMARIES IN MICRO-BIOLOGY

For some months the Secretary has been planning to secure for this Journal and its Department of Summaries, a series of papers from biologists dealing with the chief groups of microscopic plants and animals. It has not been the purpose to present a complete survey of any of the groups. The wish has been rather to bring together in one article a statement of the following things:—general biology, the method of finding, the methods of capture and of keeping alive and cultivating in the laboratory; how best to study; the general technic; the most accessible literature; and a brief outline of the classification, with keys for the identification of at least the more representative genera and species of the micro-organisms likely to be found by the beginning students in the United States.

It has been felt that the getting together of such data as this, while not a contribution to science, would be a contribution especially to isolated workers and to teachers and students in the high schools and smaller colleges.

Papers have already appeared treating the aquatic Oligochetes and the Melanconiales. The following is the third paper of the series. It is proposed to have such synopses from time to time until the more common American species of such groups as the following have been covered: The Blue-green Algae, Conjugating Algae, Diatoms, other Green Algae, Zygomycetes, Downy Mildews, Yeasts, Powdery Mildews, Hyphomycetes, Smuts, Rhizopods, Infusoria, Turbeliaria, Bryozoa, Water Mites, Entomostraca, etc.—[Editor.]

THE NATURE AND CLASSIFICATION OF PLANT RUSTS

By Frank D. Kern

1. Introduction.

The rusts are small, mostly microscopic fungi, parasitic in the tissues, especially the leaves, of the higher plants. They belong to the order Uredinales (or Uredineae) which contains without doubt the largest array of forms of any order of parasitic fungi. There is an extensive economic interest in the rusts because of the fact that they do great damage to most of the cultivated crops. Their varied spore-formation makes them at once of unusual interest to the general student with the microscope. Many species have spores of five morphological sorts. In some species these occur in regular succession upon one sort of host-plant but in many there is a striking change of hosts (known as heteroecism), a definite part of the life-cycle being produced quite apart and dissociated from the other part.

The spores are borne in more or less definite groups called sori (rarely singly), covered at least at first by overlying host tissue and set free either by early rupture or by weathering. On account of the fact that the mycelium is always wholly buried within the host

tissues it is quite natural to fall into the habit of thinking and speaking of the spore-structures, which manifest themselves upon the surface, as if they constituted the whole plant instead of representing only the reproductive portions. Although it is true that this treatment will confine itself chiefly to the spore-structures yet it is well to get the conception at the start that we must look upon the mycelium with its resulting spore-forms, in its entirety, if we would compare these little organisms with other and higher plants.

On account of the vast array of these forms, many of which have never been investigated by anyone, it is manifestly impossible to present much in the way of description of specific forms. It is hoped, however, that a statement of the main features of morphology and life-history together with their application to classification may serve to break down some of the apprehensive feelings which many now entertain toward the group as a whole. It is with this object in view that the following discussion is presented. The systematic account is confined to genera and species found in the United States.

2. Habitat and Distribution.

The rusts are strictly parasitic upon ferns and flowering plants and are liable to be found anywhere upon these hosts. Although the spores are microscopic in size, when aggregated into sori they are often conspicuous even to the naked eye and can usually be recognized easily under a hand lens. The sori may appear upon any part of the host above ground but the leaves are most commonly affected. Presence of rust may often be indicated by yellow or discolored spots upon the leaf-blades, or by swellings and galls upon the petioles and stems, or by fasciations of the branches known as witches' brooms.

In consistency the sori may be powdery (pulverulent), from the falling away of the spores, or they may be compact and firm, or in some species gelatinous. In shape and size there is great variation. Often they are roundish or oval, about 0.2-1 mm. across and more or less cushion-shaped (pulvinate); some are cup-shaped (cupulate), 0.1-0.4 mm. in diameter; others project as cylindrical, filiform, columnar, or wedge-shaped masses varying in length from 2 or 3 mm. up to 10 or 20 mm. In practically all cases the spore-mass is elevated to some extent above the surface of the host tissue and by

this means alone it is often possible to distinguish in the field between true rusts and many spot-fungi which simulate rusts in general appearance. This is especially true of grass and sedge rusts. In color the various shades of yellow and brown predominate, but some are so pale as to appear almost white, while many are dark enough to be called black.

Rusts attack plants in all sorts of physical and climatic conditions from the seashore to the summits of the highest mountains, and from the tropics to the polar regions. There is scarcely a family[1] of flowering plants in which some of the members are not affected by these parasites. In most any region where there is vegetation some rusts can be found. In the fields on wheat, oats, and other cereals; in the orchards on apples, pears, and quinces; in the gardens on asparagus and beans; in the ornamental plantings on roses, hawthorns, and cedars; in greenhouses on carnations and chrysanthemums; in the forest on pines, spruces, firs, oaks, cottonwoods, and willows; in low places and swamps on sedges and crowfoots; in semi-arid regions on sage-brush and greasewood; in wild and waste places everywhere on grasses, sunflowers, asters, goldenrods, dandelions, and hundreds of other weeds and flowers.

Because a rust is known to live upon a certain host it does not necessarily follow that the rust can be found wherever the host grows. Wild roses have several species known on them; one of these is found practically everywhere throughout the region of the hosts, while the others seem restricted to certain geographic locations, for example one is in the northeastern states, another in the prairie region of the central west, another in the Rocky Mountains and so on. Some rusts which change hosts, as indicated in a foregoing paragraph, might be expected to be limited to the region which is common to both hosts, but the fact that many of these have the capacity to maintain themselves independently on one host upsets this expectancy. A notable illustration of this is the common stem-rust of wheat which can have one stage on the barberry if any bushes are in proximity but which flourishes equally well in regions where the barberry is unknown.

1. The order Pandanales, of which the cat-tail (*Typha*) is our representative, and the Palmales, the palms, are conspicuous examples of large alliances upon which no rusts are known.

It becomes evident from the foregoing discussion that in a study of these fungi a study of the hosts is also not only important but necessary. A knowledge of the hosts is essential in classification and identification. A good way to begin is to examine and become familiar with all of the forms of rust on some particular host or closely related groups of hosts. In that way an interesting knowledge of flowering plants will be built up as the study proceeds from one group to another.

3. Collecting.

In collecting one keeps the eye on practically all of the vegetation, looking especially for discolored spots and swollen (hypertrophied) areas but does not fail to take hold of and examine closely many a plant which appears perfectly normal. A leaf or shoot which is more upright than usual is always suspicious. A hand lens is very useful and may assist greatly in forming a judgment as to whether a rust is present. Until one becomes familiar with the gross appearances of the various sori it is well to take home questionable material for microscopic examination.

It is always best to gather a fair amount of material. The importance of gathering sufficient to give some clue as to the identity of the host after the specimen has been preserved and packeted cannot be over emphasized. Flowers or some portion of the infloresence should be included whenever available, portions of the stem, unrusted leaves, basal leaves, etc., are advantageous. Care should always be taken to make sure that the rusted specimens and the portions included for host identification are from the same plant, or species, otherwise some very curious results may be obtained. Such a warning may seem unnecessary but such things have happened to experienced collectors. Some make it a point to gather separate phanerogamic specimens for the host determination but such is not necessary as a rule and is less convenient than the inclusion of smaller diagnostic portions of the host to be included with the fungous specimens.

4. Care and Cultivation.

If specimens are desired for future study only they do not require any special treatment but are best preserved by pressing

them in the ordinary method between some sort of absorbent driers. If it is desired to keep the spores alive so that they may be germinated and studied, or used for inoculating purposes, then certain precautions are necessary.

In general we may divide the spores into two classes, active and resting. The *active* class includes the cluster-cup spores, the summer or red-rust spores, and certain others such as those of the common cedar-apples. These spores are ready for germination upon maturity and will lose the power to grow unless kept in a reasonably fresh condition. If it is desired to keep them alive the parts of the host upon which they are growing should be kept as near normal as possible. In the case of small herbaceous plants often the best way is to remove them to pots, taking care to transfer a sufficient ball of earth so that the shock of transplanting will be reduced to a minimum. Oftentimes portions of the host-plant may be kept fresh for a sufficient time by placing the cut ends of stems or branches in water.

The winter or so-called black-rust condition of grass and sedge rusts furnish fine examples of the *resting* class of spores. These spores are produced in the late summer or fall and normally retain their viability through the winter and germinate in the spring. Collections made in the fall and kept in a warm dry room during the winter usually fail to germinate. The freezing temperature of the outdoor atmosphere is not detrimental. It is necessary to prevent the specimens from thoroughly drying. If put up in cheese cloth packets and tied to the branches of a shrub close to the ground the spores will usually winter over well. Resting spores collected in the field in the early spring usually show good germination. In the spring the cloth packets should be brought into the laboratory about the time conditions are favorable for growth outside. The packets may be sprayed and after a few days of warmth and moisture the spores should show signs of growth.

Germination can be nicely observed in a hanging drop culture. Ordinary tap water is used for the hanging drop. If care is taken to make the drop rather shallow it will be possible to focus with the ordinary high power. The time required for germination depends upon the conditions in which the material has been kept. The

germ-tubes may begin to show up in an hour or two. A drop culture which does not show germination in twenty-four hours may as well be discarded.

If it is desired to make an inoculation indoors some small vigorous potted plants must be available. In case it is desired to carry out such an experiment indoors for demonstration purposes it is necessary to know the species with which one is dealing in order to attempt the inoculation upon the right species of host or else the results would be very uncertain. For example there are about one hundred species of rusts on grasses in North America. It is certain that they all produce cluster cup stages on various broad-leaved plants, but the life-histories of more than half of them are still unknown. If one is conducting an investigation many trial inoculations are attempted and some of them occasionally meet with success, but for demonstration one must select forms which can be expected to produce success. A few suggestions may not be out of place here.

The black-rust spores from the stems of wheat will infect the leaves of the barberry (*Berberis*). Young barberries may be grown in pots from seeds. The grayish-black rust from the leaves of oats will inoculate the buckthorn (*Rhamnus*), which may also be grown easily from seeds. The sunflower rust does not change hosts and the spores from the dark brown sori on wintered over leaves may be transferred to young sunflower plants and will produce there the cluster-cup stage. Spores from the common large cedar-apple on the red cedar will produce abundant infection on the wild crab-apple or the cultivated apple.

For indoor experiments the spores are removed from the grasses with a knife or scapel blade and applied to the moistened leaves of the trial host. In the case of the cedar rust it is not necessary to apply the spores but merely to suspend the cedar-apple over the plant. A moist surface and a saturated atmosphere are necessary factors for the germination of the spores. In order to insure these conditions the plant is sprayed with an atomizer before the spores are sown, the parts which will not dampen being rubbed with the fingers until water will adhere. After the sowing is made the plant is placed under a bell-jar and set in a shaded position for

two or three days. The bell-jar is temporarily removed each day to permit a change of air and is sprayed on the inside with an atomizer before being replaced.

After an inoculation is made an incubation period of about a week or ten days will elapse before infection will be evident by the appearance of sori on the areas where the spores were sown. This period must be taken into account if a teacher desires to have a demonstration ready at some given time.

5. Methods for Study.

The spores of practically all species of rust make excellent objects for microscopic study by simply mounting them in a drop of water on a slide and adding a cover glass, without any treatment whatsoever. It makes little difference whether the spores are fresh or whether they are from dried specimens they will as a rule make a good mount in water. It is even possible to allow a slide to dry out and then to run water under the cover glass and secure very good results. Distilled water is preferable to tap water.

Sometimes when spores are quite old and dry they do not wet up easily or appear somewhat shrunken. A good treatment in such cases is the addition of a little lactic acid to the drop of water. This will cause the spores to round out and take on a normal rotund appearance without producing any appreciable swelling.

On account of the ease and satisfaction in making spore mounts as described in the foregoing paragraphs it is rare that there is any occasion for attempting permanent mounts of spores. For purposes of studying the structure of the sori it is often desirable to have sections and very beautiful results can be obtained by fixing fresh material, embedding in paraffin and proceeding in the ordinary way, no special precautions being necessary. It is possible, however, to secure good preparations without resorting to the cytological methods. With some practice many will find it possible to cut good free-hand sections in pith. If the specimens are dry a small portion containing the sori is soaked in very hot water—if the water comes to a boil it will do no harm. Pith soaked in alcohol is preferable to dry pith. The pith cylinder is partially split to allow the insertion of the material and then, with some water on the razor blade to float the sections, all is in readiness. The sections can be removed

with a needle or sharp wooden pick to a slide and are ready at once for microscopic examination.

6. Characters that may be used in distinguishing the species.

In the classification and identification of the rusts there are three features which are of importance (1) the microscopic character of the spores and sori, (2) the life-cycle, i. e. the number of stages in development, so far as it can be made out, and (3) the name and systematic position of the host. The first can be learned from the microscope; the second cannot always be made out, but after a little practice helpful inferences may often be drawn; while the third must depend upon the familiarity with the flowering plants, the ability to work them out, or to secure competent aid.

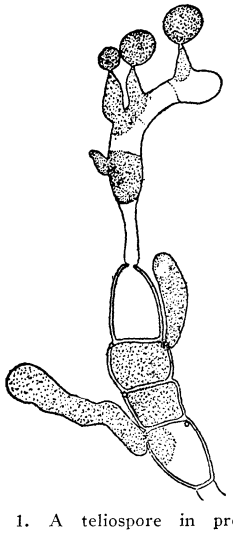

Fig. 1. A teliospore in process of germination. Two of the lower cells have young promycelia, the uppermost cell has a well advanced promycelium. This one shows the division into four basidia, three of which are shown forming basidiospores.

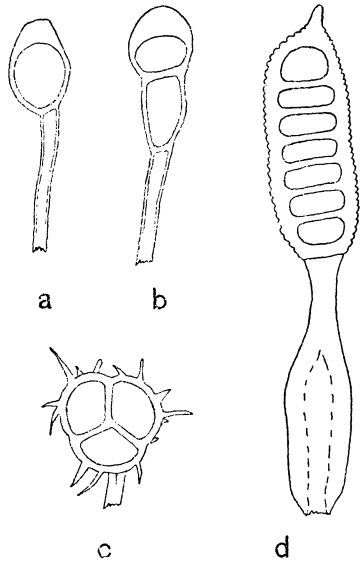

Fig. 2. Different types of free, stalked teliospores: (a) 1-celled, the wall smooth (*Nigredo Polemonii*); (b) 2-celled, the wall smooth (*Dicaeoma Grossulariae*); (c) 3-celled by oblique septa, the wall spinous; (d) several-celled by transverse septa, the wall verrucose, the pedicel swollen (*Phragmidium subcorticinum*).

The rusts usually have more than one spore stage, the differ-

ent stages or phases appearing in a definite sequence and collectively referred to as the life-cycle or life-history. Of the five morphological sorts of spores mentioned in a foregoing paragraph only four are borne in sori on the host, the fifth being of a secondary nature produced upon the germination of one of the other forms (see Fig. 1). This fifth sort, known as a basidiospore because it is produced on a basidium, is important in indicating the relationship of the rusts to other fungi but is of no importance in identfication. The basidia themselves are of importance, especially as regards their formation whether within or without the spore.

Of the four sorts of spores borne in sori only one is common to all species, this one (together with the basidiospores) comprising the full life-cycle in some species. This stage which is never lacking in any life-history is known as the *telium* (plural *telia*) and the spores as *teliospores,* sometimes called also teleutospores, and represented by the symbol III. The teliospores may be 1-several-celled (see Fig. 2), the wall may be smooth or rough but is not in any known species set with prickles (echinulate). Upon germination the teliospores produce the secondary basidiospores, which upon successful infection usually produce the *pycnial* stage, the sori being known as *pycnia* or often as spermogonia. The pycniospores are functionless so far as known and do not produce infections, but the presence of this stage is often of value in determining a life-cycle. Depending upon the life-cycle the rusts

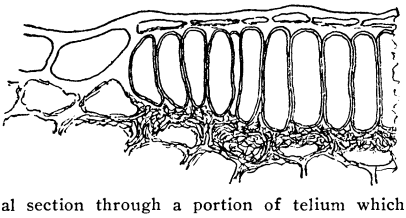

Fig. 3. A vertical section through a portion of telium which shows a single layer of spores compacted laterally. The sorus is subepidermal and the flattened epidermis is shown extending over the spores. The species represented is *Melampsora Medusae* on *Salix.*

may be divided into two groups, one with a short cycle and the other with a long cycle. In the short-cycle forms the mycelium from a basidiospore produces pycnia which are followed at once by teliospores or sometimes there is a suppression of the pycnia. The

pycnia usually appear as honey-yellow specks at first, often becoming blackish with age. The stage is often designated by the symbol O.

The long-cycle forms have the *pycnia* and *telia* and in addition have between the two either *aecia* or *uredinia* or both produced, in the order named. These two additional stages form important parts of the life-cycle.

The *aecial* stage is the so-called cluster-cup stage, deriving that name from the fact that each *aecium,* or aecidium, is in many species provided with a covering (peridium) which later opens out into a cup-like receptacle enclosing a mass of spores. The edge of this peridium often becomes toothed or fringed. In some forms the peridium becomes long and cylindrical while in others it is entirely lacking. Sometimes the aecia are encircled by clavate or capitate structures known as paraphyses (see Fig. 4, b). The aeciospores are usually borne in chains, are always 1-celled, the wall is roughened with more or less evident roundish warts (verrucose), and is in many species colorless. The symbol for the stage is I.

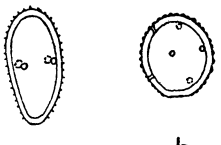

Fig. 4. (a) Showing the surface sculpturing on the side wall (longitudinal radial) of a peridial cell of *Gymnosporangium globosum*. The different species differ in the character of the markings. When in place in the peridial tissue other cells are joined end to end and side by side. (b) Showing the general nature of a paraphysis. These structures surround the spore groups in some species and in others may be intermixed with the spores.

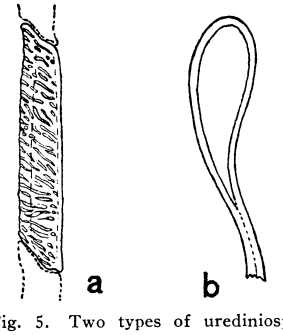

Fig. 5. Two types of urediniospores: (a) an ellipsoid spore with echinulate walls and four equatorial germ-pores (*Dicaeoma poculiforme*); (b) a globoid spore with verrucose walls and six scattered pores.

The *uredinial* stage is the one often popularly referred to as the red rust stage. In most genera the *urediniospores* (see Fig 5), or uredospores, are borne singly on pedicels in naked sori, but in some they are in chains and may be surrounded by peridia or by paraphyses. The walls of the spores are usually colored and are

always rough, either echinulate or verrucose. The spores are single-celled. Functionally these spores are repeating spores, i. e. they may reproduce themselves over and over indefinitely. The symbol for this stage is II.

The microscopic spore-characters most used are shape and size, surface markings, color and thickness of walls. In the case of teliospores the number of cells is important as is also the shape, size, and color of the pedicel which often remains attached. With regard to the urediniospores the number and location of the germ-pores are often of great value. These pores appear as lighter circular areas about 1-1.5μ in diameter and as they are the places through which the germ-tubes penetrate they are called germ-pores. The lactic acid treatment will usually assist in bringing them out more clearly than water alone. In some groups the characters of the peridial cells must be observed, especially the surface markings (see Fig. 4, a). The fine and varied character of the surface sculpturing on some of these cells almost makes them rank with diatoms as objects of microscopic interest.

7. Topics for Investigation Suitable to the General Student of the Group.

The rusts form an interesting group in which much remains to be done in the United States. One of the most fascinating and at the same time profitable opportunities for botanical students everywhere is to institute a careful study of heteroecious forms. Heteroecious species are divided into two wholly unlike halves and actual culture (inoculation) experiments are necessary to prove a relationship. In order that the work of connecting the halves may go on expeditiously, with as little unprofitable labor as possible, it is essential that the experimenter be guided by some ideas of probable relationships. These ideas can be gained in the field. The finding of aecial and telial stages in close proximity in the field is, to be sure, not proof of their affinity but is a bit of prima facie evidence. The closeness of the association, the abundance of the infection, and the occurrence of known forms must all be taken into account. Observations can best be begun in the early spring when new growth is starting. To find a tuft of grass or sedge covered with wintered over teliospores in contact with some new shoots

of a broad leaved plant bearing aecia is a strong suggestion of genetic relationship. Since in North America there are about one hundred aecial forms whose relations to telial forms are unknown it will be recognized that there is abundant opportunity for field observations. The problem may be stated from the other viewpoint by saying that there are scores of telial forms whose relations to aecia must exist but are unknown.

Some observers without greenhouse facilities may like to verify their clues by means of actual cultures. It is often possible to obtain very satisfactory results by means of outdoor cultures in a garden or other protected place. Much valuable work has been done in this way. For example, plants known to bear aecia can be transplanted to the garden and cared for until they establish themselves. During the winter rust on grass suspected of being related can be placed over the ground so that the young shoots will have to push up through it. In this way results may be obtained early before the danger of stray infections is so great. If more than one such experiment is tried in the same garden much care must be observed to prevent cross infections which might lead to confusion.

8. Systematic (General).

Teliospores compacted laterally into flattened, cushion-like masses (see Fig. 3), or filiform, columnar masses (rarely solitary within the tissues), without stalks.

Walls of teliospores gelatinous, especially at apex, dividing internally into four basidia. Family 1. Coleosporiaceae.

Walls of teliospores firm, without internal division of contents. Family 2. Uredinaceae.

Teliospores free (see Fig. 2) or united in bundles, stalked, the walls firm, or with an outer hygroscopic layer. Family 3. Aecidiaceae.

Some authors include the first two families in one under the name Melampsoraceae, and use the name Pucciniaceae for the third instead of Aecidiaceae as given above.

9. Systematic (Special).

FAMILY 1. COLEOSPORIACEAE

This family contains only one genus of importance, *Coleospor-*

ium, with about 24 species. The genus has all four spore-stages. All the species are heteroecious, the aecia being the blister rusts on the leaves (not on the twigs or bark) of pine trees (*Pinus*). The uredinia are yellowish and powdery; the telia form waxy cushions; the teliospores germinate upon maturity in the fall and the internal division of the contents into four basidia can generally be observed with the microscope without difficulty. The following common species may be mentioned.

Coleosporium Ipomoae (Schw.) Burr. on *Ipomoea,* urediniospores with uniformly thin wall 1-1;5μ; *C. Campanulae* (Pers.) Lev. on *Campanula,* urediniospores with uniformly thick wall, 2-3.5μ; *C. Vernoniae* B. & C. on *Vernonia,* urediniospores with wall 1-2μ at sides, often 2-5μ above; *C. Solidaginis* (Schw.) Thüm. on *Aster, Euthamia,* and *Solidago,* urediniospores with uniform wall, about 1-2μ. The urediniospores of the different species do not vary much in size, averaging 14-22x20-30μ.

FAMILY 2. UREDINACEAE

This family is represented in North America by seventeen or eighteen genera and a considerable number of species. In the United States only seven of these genera are common, the others being chiefly from tropical regions.

KEY TO THE PRINCIPAL GENERA

Teliospores in definite and limited sori, usually on the leaf-blades; urediniospores rounded.
- Telia conspicuous, raising or breaking through the epidermis, teliospores 1-celled.
  - Telia in the form of cushion-like masses; urediniospore-wall verrucose.
    - Teliospores in a single layer; urediniospores with intermixed paraphyses.....Genus *Melampsora*
    - Teliospores in chains; uredinia with a delicate peridium or naked.....Genus *Melampsoropsis*
  - Telia extruding as long filiform columns; urediniospore-wall echinulate.....Genus *Cronartium*
- Telia inconspicuous, in a layer in the epidermal cells or just below them, teliospores 2-4-celled.
  - Teliospore-wall brownish; uredinial peridium opening with a definite orifice surrounded by longer cells, urediniospores echinulate.....Genus *Pucciniastrum*
  - Teliospore-wall colorless; uredinial peridium without definite orifice, the cells longer at the sides and shorter toward apex, urediniospores verrucose.....Genus *Hyalopsora*

Teliospores solitary, or in very loose groups, usually buried within the parenchymal tissues; urediniospores pointed.....Genus *Uredinopsis*
Teliospores forming continuous layers around elongated and thickened stems, not erumpent; uredinial stage lacking.....Genus *Calyptospora*

GENUS MELAMPSORA CAST.

A prior name for this genus is *Uredo*. But as that word has been in general use as the name of a stage, the one called in this paper the uredinial stage, and its restriction to a true generic application might lead to confusion, a later and more commonly used name is here maintained.

The genus contains both heteroecious and autoecious species. The aecia have no peridium.[2] A conspicuous feature of the uredinia are the numerous, large paraphyses. Both aeciospores and urediniospores have colorless, verrucose walls. There are three common species.

Species

M. Medusae Thüm. Urediniospores smooth on two sides which are thickened, I on *Larix,* II and III on *Populus.*

M. Bigelowii Thüm. Urediniospores with walls evenly thick and evenly verrucose, I also on *Larix,* very similar to the preceding, II and III on *Salix* (see Fig. 3).

M. Lini (Schum.) Desm. Autoecious, on *Linum.*

GENUS MELAMPSOROPSIS (SCHROT.) ARTH. (Sometimes included in CHRYSOMYXA).

Found in its uredinial and telial stages only on the order *Ericales.* The aecia so far as known occur on the leaves or cones of spruces (*Picea*). Several of the species are rather rare. *M. Pyrolea* (DC.) Arth. on wintergreen (*Pyrola*) is common. There are two species on Labrador tea (*Ledum*); *M. ledicola* (Peck) Arth. with the II and III on the upper side of the leaves, urediniospores moderately large, 18-29 x26-36μ, wall 2.5-3μ thick; and *M. abietina* (A. & S.) Arth. with sori on the under surfaces of the leaves, urediniospores moderately small, 14-22 x20-30μ, wall 1.5-2.5μ thick. A uredinial stage on *Cassandra calyculata,* which is very rarely accompanied by telia, is *M. Cassandrae* (P. & C.) Arth.

GENUS CRONARTIUM FRIES.

A very striking genus in the telial stage on account of the long (0.5-3 mm.) filiform spore-columns. Cultures have proven that

2. The term caeoma is often applied to such forms, i. e. to aecia in which the peridium is lacking.

the aecial stages are the blister rusts of the twigs, branches and trunks of pines (*Pinus*).

Species

C. Comptoniae Arth. A common form along the north Atlantic coast on the sweet gale (*Myrica Gale*) and sweet fern (*M. asplenifolia*).

C. Quercuus (Brond.) Schröt. is widely distributed on various species of oak (*Quercus*). The aecial stage (called *Peridermium cerebrum* Peck) on pines forms globoid swellings of the branches upon which the orange-yellow aecia are arranged in a cerebroid fashion.

C. ribicola Fisch. de Waldh. is a rather recent importation from Europe and is a very serious disease of white pine (*Pinus strobus*) seedlings. The telial stage on *Ribes* (currants) is also appearing in this country.

GENUS PUCCINIASTRUM OTTH.

The characteristic feature of this genus is the hemispherical or subconical peridium of the uredinial stages with a pore-like orifice at apex surrounded by elongated cells, which are often echinulate above. Owing to the fact that the telia remain covered (indehiscent) they are somewhat difficult to study, and the partitions of the teliospores being vertical are not readily made out. Of the nine or ten species the following are the more common ones, others may be found upon *Hydrangea, Rubus, Arctostaphylos,* and *Vaccinium.*

Species

P. Agrimoniae (Schw.) Tranz. Common on *Agrimonia* from New England to North Dakota southward to Florida and Mexico.

P. pustulatum (Pers.) Diet. Widely distributed, especially northward on various species of *Epilobium.*

P. Pyrolae (Pers.) Diet. on *Pyrola* and *Chimaphila,* can be distinguished from the *Melampsoropsis* on *Pyrola* by the nature of the uredinial peridium and the echinulate markings of the urediniospores.

GENERA HYALOPSORA MAGN. and UREDINIOPSIS MAGN.

These genera include all of the rusts which are known on ferns in America. The cycle of development in both genera is not well understood. Both have two spore-forms

known on the fern-hosts aside from the telia. Some authors have looked upon one of these forms as aecia and the other as uredinia but evidence is lacking to prove the correctness of this assumption and recent work[3] indicating the heteroecious character of certain species of *Uredinopsis* throws some doubt upon that disposition. For the most part the two genera occur upon different genera of ferns; *Hyalopsora* on *Phegopteris, Cystopteris, Polypodium,* and *Pellaea; Uredinopsis* on *Osmunda, Onoclea, Pteridium, Asplenium,* and *Dryopteris.* The two genera can be further separated by the fact that one of the spore-forms of *Uredinopsis* has fusiform spores which are acute or beaked above, with a wall which is smooth except for two longitudinal ridges bearing single rows of minute projections, while both spore-forms in *Hyalopsora* have rounded spores with evenly verrucose walls. *H. Aspidiotus* (Peck) Magn. is the most widely distributed of the four species belonging to that genus; *U. Osmundae* Magn. on *Osmunda, U. mirabilis* (Peck) Magn. on *Onoclea,* and *U. Atkinsonii* Magn. on *Asplenium* and *Dryopteris* are the best known of the seven described species of *Uredinopsis.*

GENUS CALYTOSPORA Kühn.

Only one species is at present recognized in this genus, *C. columnaris* (A. & S.) Kühn (*C. Goeppertiana* Kühn). Uredinia are lacking; the telia are found on *Vaccinium,* and the aecia on the balsam fir (*Abies balsameum*) in this country. The telia form an even, polished, reddish-brown layer around the elongated and enlarged stems; the teliospores are closely packed in the epidermal cells, the wall of each spore very thin at the sides 0.5-0.8μ, somewhat thicker above 1-1.5μ.

FAMILY 3. AECIDIACEAE
(Called also PUCCINIACEAE)

In this family belong the largest number of rusts, including for the most part those that cause serious injury to economic plants. The number of genera to be dealt with is dependent upon the scheme of classification which one follows. According to the old method any species of the group having free teliospores would belong to the genus *Puccinia* if it possessed a single other character, i. e. two-celled teliospores (see Fig. 2, b). Likewise those forms would belong to *Uromyces,* which possess one-celled teliospores (see Fig. 2, a). Such a scheme, based on only one character, brought together, as a genus, species of the most diverse forms and varied affinities. A classification which takes into consideration the nature of the spore-wall, germ-pores, the origin of the sorus, i. e. whether under the cuticle or under the epidermis, the life-cycle, whether one or more stages are lacking, and other important characters will, of course, segregate the species usually placed under *Puccinia*

3. Fraser, W. P. Science, N.S. 36:595. 1912.

and *Uromyces* and increase the number of genera, but it will have the very great advantage of forming groups which have some affinities. Following such a system we have among the more common forms in the United States about twelve genera to consider in the place of two, but this number might be decreased nearly one-half by not recognizing the purely artificial character of number of cells as a basis for generic separation. The present state of knowledge does not seem sufficient, however, to warrant such a change.

KEY TO THE PRINCIPAL GENERA

Teliospores or pedicels, or both, more or less united; uredinia when present naked but often with intermixed paraphyses.
- Teliospores united into a head, or cushion-like body, on a compound pedicel ..... Genus *Ravenelia*
- Teliospores free but borne in groups of two to eight on a common stalk.
  - Life-cycle with all spore-forms..... Genus *Tranzschelia*
  - Life-cycle with pycnia and telia..... Genus *Polythelis*

Teliospores and pedicels both free; uredinia when present without peridium but sometimes with encircling paraphyses.
- Teliospores becoming imbedded in masses of jelly formed by gelatinization of the pedicels, teliospore-pores varying in number and arrangement; uredinia lacking..... Genus *Gymnosporangium*
- Teliospores in definite sori, not becoming gelatinous.
  - Pycnia subcuticular, other sori subepidermal; teliospore-pores when more than one in a cell lateral; uredinia usually with encircling paraphyses.
    - Teliospore-wall more or less conspicuously laminate.
      - Teliospores 2-celled, the wall finely and sparsely verrucose ..... Genus *Uropyxis*
      - Teliospores 2 to several-celled, more or less coarsely verrucose or even smooth.
        - Life-cycle with all spore-forms..... Genus *Phragmidium*
        - Life-cycle with pycnia, aecia and telia..... Genus *Earlea*
    - Teliospore-wall not noticeably laminate.
      - Teliospore-wall spinous, teliospores 3-celled by oblique septa..... Genus *Nyssopsora*
      - Teliospore-wall nearly or quite smooth, the spores 2- or several-celled by transverse septa.
        - Teliospores 2-celled..... Genus *Gymnoconia*
        - Teliospores 3-13-celled..... Genus *Kuehneola*

Pycnia and other sori subepidermal; teliospore-pores one in a cell and apical; uredinia rarely with encircling paraphyses.
Life-cycle with all spore-forms.
Teliospores 1-celled .....Genus *Nigredo*
Teliospores 2-celled .....Genus *Dicaeoma*
Life-cycle with pycnia, aecia and telia.
Teliospores 1-celled .....Genus *Uromycopsis*
Teliospores 2-celled .....Genus *Allodus*
Life-cycle with pycnia, uredinia and telia.
Teliospores 1-celled .....Genus *Klebahnia*
Teliospores 2-celled .....Genus *Bullaria*
Life-cycle with pycnia and telia, or only telia.
Teliospores 1-celled .....Genus *Telospora*
Teliospores 2-celled .....Genus *Dasyspora*

GENUS RAVENELIA BERK.

This genus is especially characterized by the manner in which the teliospores are fascicled on compound pedicels. The spores form heads which are bordered by hyaline cysts that swell more or less in water. The urediniospores are often paler below. The genus occurs, with the exception of one species, upon leguminous hosts included in the families, Mimosaceae, Caesalpiniaceae, and Fabaceae. The exception is on *Phyllanthus* belonging to the Euphorbiaceae. Thirty-eight species have been described in North America, chiefly from Mexico, Central America, and the West Indies. Several occur along the southern border of the United States but only one comes into the central and northern states, *R. epiphylla* (Schw.) Diet. on *Cracca* (*Tephrosia*).

GENUS TRANZSCHELIA ARTH.

A small genus, only two species at present known. The urediniospores have the wall thicker and less echinulate above. The teliospores are 2-celled and a characteristic feature about them, aside from the manner in which they are borne, is the ease with which the two cells separate. One species, *T. cohaesa* (Long) Arth., known only from Texas, is autoecious on *Anemone decapetala;* the other, *T. punctata* (Pers.) Arth., is widespread and heteroecious, O and I on *Anemone, Hepatica,* and *Thalictrum,* II and III on peaches, cherries, and plums.

GENUS POLYTHELIS ARTH.

A small genus which is confined to hosts of the family Ranunculaceae. The teliospores are very similar to those of *Tranzschelia* but the two genera differ very markedly in the life-cycle. A species having both cells of the teliospores globoid is *P. fusca* (Pers.) Arth. on *Anemone quinquefolia* common east of the Mississippi; another with the lower cell considerably elongate, on *Pulsatilla hirsutissima,* is *P. Pulsatillae* (Rostr.) Arth. common from the Mississippi to

Colorado and Montana; and a third with the lower cell somewhat elongate, on *Thalictrum,* is *P. Thalictri* (Chev.) Arth., distributed throughout the northern United States and Canada.

GENUS GYMNOSPORANGIUM HEDW. F.

Characterized, with a few exceptions, by a dingy-white, membranous peridium, which elongates into a tubular form and tends to rupture along the sides; by large peridial cells usually conspicuously sculptured on the inner and side walls (see Fig. 4, a); by aeciospores with colored walls and evident germ-pores[4]; and by teliospores with hyaline pedicels of considerable length, the outer portions of which swell in moisture and become gelatinized to form a jelly-like matrix in which the spores appear imbedded. As regards hosts the genus is restricted in its aecial stage to the family Malaceae (Pomaceae), with three known exceptions, and in its telial stages to the Juniperaceae without any known exceptions. About thirty species have been reported in the United States, of which the following are most likely to be collected.

Species

G. Juniperi-virginianae Schw. (*G. macropus* Link). The common "orchard rust" forming globoid galls on the Virginia red cedar in the telial stage and attacking crabapples and cultivated apples in the aecial stage. The telia on the galls are cylindrical, the galls die after producing a crop of telia.

G. globosum Farl. Also forming telia on the red cedar but chiefly on the genus *Crataegus* in its aecial stage. The telia are wedge-shaped and the mycelium in the galls is perennial, producing new telia between the scars of the sori of previous seasons.

G. germinale (Schw.) Kern (*G. clavipes* C. & P.). The hemispherical telia in this species do not form galls but long gradual enlargements of the twigs or branches. The aecia attack the fruits and often the twigs of *Cydonia* (quince), *Amelanchier, Aronia,* and *Crataegus.* The peridium is unusually whitish. The telia occur not only on the red cedar (*Juniperus virginiana*) but also on the junipers (*Juniperus communis* and *J. siberica*).

Along the Atlantic coast are two conspicuous species on the branches of

4. In most genera germ-pores are apparently wanting or obscure in the aeciospores but are usually evident in the urediniospores and teliospores.

the white cedar (*Chamaecyparis thyoides*); *G. Ellisii* (Berk.) Farl. with yellowish filiform telia and *G. Botryapites* (Schw.) Kern with brownish pulvinate sori. *G. Betheli Kern* is a gall form very destructive to the red cedar (*J. scopulorum*) in the Rocky Mountains; *G. juvenescens* Kern in the same region causes witches' brooms on the cedars.

GENUS UROPYXIS SCHRÖT.

A genus usually separable from all others here described by the laminate wall of the teliospores, the outer layer of which is gelatinous, swelling in water. The species are more common southward into Mexico. *U. sanguinea* (Peck) Arth. on *Mahonia* (*Berberis*) is distributed throughout the western mountain region from Washington and Wyoming south to Guatemala. *U. Amorphae* (Curt.) Schröt. on *Amorpha* is widely distributed over the United States and especially abundant in the Mississippi valley. In the former the gelatinous outer layer is relatively inconspicuous, in the latter 1-3μ thick at apex and base of spores and 7-15μ at the sides.

GENUS PHRAGMIDIUM LINK.

The cycle of development in this genus includes all sporeforms and all species are autoecious. For hosts it is restricted to a single family, the Rosaceae. The aecia and uredinia are both without peridium but usually with encircling paraphyses (see Fig. 4, b). The teliospores are usually more than two-celled by transverse septa (Fig. 2, d). Sixteen species have been described in North America, four on the tribe Rubeae, eight on the tribe Roseae, and four on the Potentilleae. *P. imitans* Arth. on *Rubus strigosus* is the most widely distributed of the first group. *P. disciflorum* (Tode) James and *P. subcorticinum* (Schrank) Winter are common on cultivated roses in many parts of the United States, especially the northern states east of the Rocky Mountains. The teliospores of the former are 5-9-celled, with walls blackish-brown, opaque, 5-7μ thick, of the latter 5-7-celled, the walls chestnut-brown, not very opaque, 3-5μ thick; in both species the teliospore-walls are verrucose and the pedicels swell in water. *P. Andersoni* Shear on *Dasiphora fruticosa* and *P. Potentillae* (Pers.) Karst. on various species of *Potentilla* are representatives of the third group. In *P. Andersoni* the teliospores are furnished with a hyaline papilla at the apex and the pedicel is much swollen in the lower part, while in the other the apex has no apiculus and the pedicel is not swollen.

GENUS EARLEA ARTH.

This genus resembles *Phragmidium* but the cycle of development includes only pycnia, aecia, and telia. Several species have been referred here but only one of them is common, that on various roses. This species differs from the species of *Phragmidium* common on roses by the teliospores having smooth walls and pedicels not swelling in water and also by the fact that the telia are large and appear always upon the stems, while in that genus they are small and only upon the leaves.

GENUS NYSSOPSORA ARTH.

The teliospores differ from those of all other genera (except *Triphragmium*) in having the teliospores divided into cells by oblique partitions in such a way as to make them triangularly 3-celled (Fig. 2c). They differ from *Triphragmium,* which is not discussed in this paper, by the short life-cycle and the spinous character of the teliospore walls. Only one species, *N. clavellosa* (Berk.) Arth. on *Aralia nudicaulis* is known east of the Rocky Mountains; another in the western mountainous region is *N. echinata* (Lev.) Arth. on *Ligusticum* and *Oenanthe.*

GENUS GYMNOCONIA LAGERH.

Here belongs the orange rust of blackberries and raspberries (*Rubus* spp.) which is so well known. It is the only species of importance and is best known under the name *G. interstitialis* (Schlecht.) Lagerh. The pycnia and aecia are the conspicuous stages; no uredinial stage exists.

GENUS KUEHNEOLA (LINK) ARTH.

Another genus with several species on the Rosaceae but differing from those already described on that family. The teliospores are smooth and few- to many-celled by transverse partitions. The aecial stage is lacking. *K. obtusa* (Strauss) Arth. with 3-5-celled teliospores is a common form on *Potentilla canadensis; K. uredinis* (Link) Arth. with 5-13-celled (usually 5-6) teliospores is another rust of *Rubus,* but is not at all conspicuous and can not be confused with *Gymnoconia.* One species, *K. Gossypii* (Lagerh.) Arth., is a rust of the cotton plant known from southern Florida and the West Indies.

GENUS NIGREDO ROUSS.

To this and the following seven genera belong most of the species formerly referred to the old composite genera *Uromyces* and *Puccinia.* By the use of the generic names here adopted the important information concerning the life-cycle is conveyed in the name without the necessity of the roundabout method of explaining the status with a phrase.

The aecia are usualy cupulate, aeciospores borne in chains with colorless, verrucose walls; the uredinia are without peridium or encircling paraphyses, urediniospores borne singly on pedicels, the walls colored, echinulate or verrucose, the pores variously arranged; the telia are sometimes long covered by the epidermis, teliospores free, stalked, 1-celled (see Fig. 2a), the wall firm, colored, smooth or verrucose, with one apical pore. The genus *Nigredo* is represented by a large number of species, many of which are common in the United States. It will be possible to mention only a few of those most likely to be found.

Species

Host belonging to grass family (Poaceae).

Urediniospore-pores 3 or 4, equatorial, the spores medium-sized (15-19 x18-23μ); on species of *Panicum,* chiefly *P. virgatum;* I unknown. .....*N. graminicola* (Burr.) Arth.

Urediniospore-pores about 8, scattered, the spores large (19-27x25-37μ); on species of *Spartina;* I on *Steironema, Polemonium, Phlox,* and *Collomia*.....*N. Polemonii* (Peck) Arth.

Host belonging to sedge family (Cyperaceae).

Urediniospore-pores 4, equatorial; on *Scirpus;* I on *Cicuta* and *Sium* .....*N. Scirpi* (Cast.) Arth.

Urediniospore-pores 2, above the equator; on Carex; I on *Aster* and *Solidago*.....*N. perigynia* (Hals.) Arth.

Host belonging to family Araceae; urediniospore-wall thicker above, pores 4; on *Caladium;* autoecious.....*N. Caladii* (Schw.) Arth.

Host belonging to family Juncaceae; urediniospore-pores 2, equatorial; on *Juncus;* I on *Ambrosia, Arnica,* and *Cirsium*.....*N. Junci* (Desm.) Arth.

Host belonging to family Polygonaceae; urediniospore-pores 4, equatorial; on *Polygonum;* autoecious.....*N. Polygoni* (Pers.) Arth.

Host belonging to family Carophyllaceae; urediniospore-pores 3 or 4, equatorial; on *Dianthus* (carnation); I on *Euphorbia* (not known in United States).....*N. caryophyllina* (Schrank) Arth.

Host belonging to family Fabaceae.
Urediniospore-pores 3-6, scattered; on *Trifolium pratense* (red clover); I unknown.....*N. fallens* (Desm.) Arth.
Urediniospore-pores 3 or 4, equatorial; on *T. repens* (white clover; autoecious.....*N. Trifolii* (Hedw. f.) Arth.
Urediniospore-pores 2, equatorial; on *Strophostyles, Vigna,* and *Phaseolus* (including the garden bean); autoecious.....*N. appendiculata* (Pers.) Arth.
Host belonging to family Asclepiadaceae; urediniospore-pores 4, equatorial; on *Asclepias;* I unknown.....*N. Howei* (Peck) Arth.

GENUS DICAEOMA S. F. GRAY.

This genus resembles *Nigredo* in every important character, differing only in having teliospores with two cells. It is without doubt the largest of the rust genera. Here belong the bulk of grass and sedge rusts, including the important cereal rusts. Dicotyledonous plants of eighty or ninety genera representing about twenty-five families serve as hosts for species of this genus, but most of these are not of economic interest or of common occurrence.

Species

Host belonging to grass family (Poaceae).
Telia early naked, blackish, chiefly on the culms and sheaths; urediniospore-pores 4, equatorial; on wheat, oats, rye, timothy and several wild grasses (*Agrostis, Agropyron, Elymus*); I on barberry.....*D. poculiforme* (Jacq.) Kuntze (=*Puccinia graminis* Pers.)
Telia long covered by the epidermis, often grayish-black; chiefly on the leaf-blades.
Urediniospore-wall brown; the pores about 6, scattered.
Urediniospores with intermixed paraphyses; telia rarely formed in our region; on species of *Poa,* common on blue-grass; I on *Tussilago,* rare.....*D. epiphyllum* (L.) Kuntze (=*Puccinia poarum* Niels.)
Urediniospores without paraphyses; teliospores germinating in the fall; on rye (*Secale cereale*); I on *Lycopsis,* not yet found in America.....*D. Asperifolii* (Pers.) Kuntze (=*Puccinia rubigo-vera* DC.)
Urediniospore-wall yellow or colorless.
Teliospores with finger-like projections at the apex; on oats and wild grasses (*Cinna, Holcus* and others); I on buckthorn (*Rhamnus*).....*D. Rhamni* (Pers.) Kuntze (=*Puccinia coronata* Cda.)

Teliospores with smooth apex; on wheat; I unknown.....
.....*D. triticina* (Erikss.) Kern.
(=*Puccinia triticina* Erikss.)

Host belonging to sedge family (Cyperaceae).
Urediniospore-pores 3 (in occasional spores 4), equatorial.
Urediniospores large (18-26x24-39μ); teliospores large (39-71μ long); on species of *Carex;* I on *Urtica*.....*D. Urticae* (Schum.) Kuntze
Urediniospores medium-sized (15-21x19-25μ); teliospores medium-sized (37-58μ long; on *Carex;* I on *Ribes*.....
.....*D. Grossulariae* (Schum.) Kern.
(=*Puccinia Grossulariae* (Schum.) Lagerh.
Urediniospore-pores 2, in the upper part of spore.
Urediniospores medium-sized (15-19x19-24μ); teliospores medium-sized (35-50μ long); on *Carex;* I on *Aster, Solidago,* and *Erigeron*.....*D. Erigeronatum* (Schw.) Arth.
Urediniospores large (17-21x23-32μ); teliospores large (42-65μ long); on *Carex;* I on *Sambucus*.....*D. Sambuci* (Schw.) Arth.
Host belonging to composite family, genus *Helianthus;* autoecious.....
.....*D. Helianthi* (Schw.) Kuntze

GENUS UROMYCOPSIS (SCHRÖT.) ARTH.

The character of the pycnia, aecia, and telia are essentially like the genus *Nigredo,* but the uredinial stage is wanting. The telia often arise within the aecia or about them from the same mycelium. A good example of the genus is *U. Psoraleae* (Peck) Arth. on various species of *Psoralea* from Minnesota, Illinois and Texas westward to the Pacific coast. The genus is more common westward.

GENUS ALLODUS ARTH.

This genus bears the same relation to *Dicaeoma* that *Uromycopsis* does to *Nigredo. A. Podophylli* (Schw.) Arth. is a common and widely distributed species, occurring on *Podophyllum peltatum.* The teliospore-walls of this species are especially interesting on account of the straight or curved conspicuous spines with which they are beset.

GENUS KLEBAHNIA ARTH.

No cupulate aecia are present in this genus, the pycnia being followed by a stage of the uredinial-type. Only a few species have been referred here of which the more common one is *K. Glycyrrhizae* (Rabh.) Arth. on *Glycyrrhiza.* This is found from North Dakota and Kansas westward.

GENUS BULLARIA DC.

Resembling *Klebahnia* except for the possession of teliospores having two cells. A widespread species is on various members of the family Cichoriaceae, *Hieracium, Agroseris, Nothocalais,* and *Crepis,* for which the oldest name seems to be *B. Hieracii* (Schum.) Arth. The teliospore-walls are finely verrucose and uniformly thick, 1-1.5μ. Another species on false boneset (*Kuhnia*) is *B. Kuhniae* (Schw.) Kern (*Puccinia Kuhniae* Schw.) with teliospore-walls smooth and thicker above, 3-4μ at sides, 5-7μ above.

GENERA TELOSPORA ARTH. and DASYSPORA B. & C.

To these genera belong species with short life-cycles. In some the teliospores germinate only after a resting period (micro-forms), in others they germinate at once (lepto-forms). The telia are usually compact and arranged in circinating or crowded groups. Most specimens showing teliospores germinating upon maturity can be placed here with considerable confidence, as they very rarely belong to genera with other spore-forms in the life-cycle. The 1-celled forms belong to *Telospora,* and the 2-celled forms to *Dasyspora.* Only a few species are known in the former genus. *Telospora* Rudbeckiae (A. & H.) Arth. on *Rudbeckia laciniata* is the most likely to be met with. *Dasyspora* is a large genus. *D. Anemones-Virginianae* (Schw.) Arth. on *Anemone* and *D. Xanthii* (Schw.) Arth. on *Xanthium* are of common occurrence.

FORM-GENERA

In addition to the forms of known life-cycle, which may be referred to true genera, there are many forms whose life-cycle is too imperfectly understood to permit them to be placed with confidence in any of the known genera. Many of these can be recognized merely as a stage and judging from analogy it is safe to assume that they cannot be independent but must be associated with other stages. In order that such forms may have names so that they may be discussed more easily the practice has grown up of using certain terms as if they were really generic names, when in fact they represent only stages. For example aecial forms of the usual cluster-cup type whose connections are unknown are placed under *Aecidium;* aecial forms of the blister-type inhabiting the pine family

(Pinaceae) are treated by most writers under *Peridermium;* while aecial forms lacking a peridium are considered under *Caeoma.* Uredinial and other similar looking stages are referred to *Uredo.* These names which are accorded generic treatment, but which include only isolated stages, are referred to as *form-genera,* and as such they serve a useful purpose in disposing of the residue of imperfectly known forms.

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